

HELIAMPHORA EXAPPENDICULATA, A CLEARLY
DISTINCT SPECIES WITH UNIQUE CHARACTERISTICS

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Introduction

Due to its remoteness and inaccessibility, the flora of the Guyana Highlands, in the south of Venezuela, remained nearly completely unexplored until as recently as only 50 years ago. Before that time, only a few expeditions had reached the tepuis in the area, e.g. Roraima (Im Thurn 1885), Duida (Gleason 1931) or Auyan (Gleason 1939). The botanical collections from these expeditions were amazing (Im Thurn 1886)—the flora is spectacular even in the extensive savannahs around the tepuis (Schomburgk 1931).

In 1946, another pioneer in the exploration of the tepuis, Felix Cardona, explored Apacara-tepui (a part of Chimanta-tepui). On this trip he observed and collected material of an interesting *Heliamphora* (Cardona 51648).

At approximately the same time, two groups of botanists started to explore this vast area more systematically. One group was led by Julian A. Steyermark, who started his career at the Chicago Natural History Museum. Later on, he became so fascinated in the botany of this extraordinary region that he spent 25 years of his life in Venezuela. In 1984 he returned to the USA to the well-known Missouri Botanic Garden. Never before or afterwards had anyone made so many botanical collections as Steyermark. The other group was from the New York Botanical Garden and was led by Bassett Maguire with the collaboration of John J. Wurdack. One of the largest tepuis, with a surface of 615 km², the huge area of Chimanta-tepui was at that time unexplored. Steyermark and Wurdack made independent expeditions to reach its top in 1953 (Steyermark 1955). Due to its remoteness, Steyermark needed months to reach the top. Wurdack reached the top of Chimanta-tepui on 29 January 1953. He collected material of this region's interesting *Heliamphora* (Wurdack 34262; this material is used as the type for the species described in this paper) on the northwest slopes of Churi-tepui, another part of the huge Chimanta-massif. In the same year, Bernardi organized an expedition to reach the top of Aprada-tepui, an isolated tepui near and to the north of Chimanta. Even though he failed in this goal, he was able to collect material (Bernardi 796) of the same *Heliamphora* species at the base of this tepui. In 1955, Steyermark and Wurdack made another expedition to the Chimanta-massif, and collected yet additional material of this new *Heliamphora*.

After these collections, this taxon was observed only very rarely. In 1978 it was described as a variety of *H. heterodoxa* by Maguire (Maguire 1978). Between 1983 and 1986, Huber organized several helicopter-expeditions to the Chimanta-massif and performed intensive botanical and geological explorations. But in the book where he presented the results of these expeditions (Huber 1992) he never mentioned the distinctive plant. It seems that it was overlooked due to its habitats which are both remote and difficult to access.

Heliamphora exappendiculata (Maguire & Steyermark) Nerz & Wistuba *comb. et stat. nov.*

(Memoirs of the New York Botanical Garden (Vol. 29, 1978): The Botany of the Guyana Highland - Part X: p. 54)—‘*Var heterodoxi simili sed amphoris sine appendicibus*’

Holotype (NY): Venezuela, 29.01.1953, John J. Wurdack 34262.

Rhizomes branching, plants often forming dense colonies. Plants growing in or below



Figure 1: Herbarium specimen 34262 (NY), holotype for *Heliamphora exappendiculata*. Image provided courtesy of the New York Botanical Garden.

vertical cliffs, with the rhizomes growing down, turning upwards and bearing pitchers. Below the cliffs, the rhizomes grow upwards normally. Pitchers ventricose in the lower part, 12-25 cm long, 4-10 cm wide at the upper part. The outer surface of the pitchers loosely covered with simple minute trichomes. The inner surface of the upper part of the pitcher densely covered with fine hairs. The lid completely embedded in the apex of the pitcher, circular to ovate, 5-10 mm long, usually pointed in the apex, approximately forming a small triangle at the inner side roughly. Outer surface of the pitcher covered with short trichomes. Colour of the pitcher pale green, in sunny places it may develop irregular red dots or completely red pitchers. Sometimes the pitchers are green in the lower part and red in the upper part, especially on the inner pitcher surface. Lid usually red, slightly hairy at the outer part. 1-3 flowers. Inflorescence about 40 cm long, peduncle 3-5 cm long, glabrous; bracts 3-4 cm long, bearing rudimentary pitchers. Tepals 4, oblong-lanceolate, 3-5 cm long, 1.5-2 cm wide, white to whitish-pink; 10 stamens in 1 series, filaments 7 mm long, anthers oblong, lanceolate, 8 mm long, 1.2 mm wide. Ovary 3-celled, pubescent, style glabrous. Seed approximately 2 mm long, compressed, ovate, irregularly winged.

Specimens Examined

Churi-tepui (Muri-tepui), 2050 m, 29.01.1953, John J. Wurdack 34262, Holotype (NY); Churi-tepui (Muri-tepui), 2050 m, 29.01.1953 Wurdack No. 34262, ISOTYPE (K); Churi-tepui (Muri-tepui), 2250-3000 m, 26.01.1953 Wurdack No. 34236 (VEN); Churi-tepui, 2100-2200 m, 24.01.1953, Wurdack No. 34172 (VEN); Aprada-tepui, 1000-1100 m, 18.08.1953, Bernardi No. 796 (VEN); Chimanta-massif, Central Section, 1925 m, 5.2.1955, Steyermark & Wurdack No. 441; Torono-tepui, 1875-1950 m alt; 26.02.1955, Steyermark & Wurdack No. 1135 (VEN); Apacapa-tepui, 2125-2300 m, 13.04.1953 Steyermark No. 74888 (VEN, K); Apacara-tepui, 1900 m, 08.07.1946, Cardona No. 51648 (VEN); Amuri-tepui, 1850 m (+/-), 2-5.2.1983, Steyermark *et al.* No. 128489 (VEN).

Geology and Geography

Heliamphora exappendiculata is apparently restricted to Chimanta-tepui and Aprada-tepui (Brewer-Carias 1987), two sandstone-plateaus at the centre of the Gran Sabana. Chimanta is one of the largest tepuis; it is characterized by many dissections, valleys and ravines at the plateau-area. Aprada is smaller than Chimanta and is located close to it in the north-west. It consists of two plateaus, both relatively flat which are divided by a valley. *Heliamphora exappendiculata* seems to be adapted to this high degree of vertical cliffs of Chimanta-tepui, where it grows with few other plants. Due to the diversity of the surface of Chimanta-tepui, many different habitats can be found on the plateau (including vast savannahs, shrubby forests, dry cliffs, wet cliffs and many rivers and waterfalls). It is because of this great diversity of habitats, that three different species of *Heliamphora* exist side by side at the top of Chimanta-tepui, *Heliamphora exappendiculata*, *H. pulchella* and *H. chimantensis*. On Aprada only two species of *Heliamphora* have been recorded so far, *Heliamphora exappendiculata* and *H. pulchella*. Here *Heliamphora exappendiculata* was not found growing on cliff faces but rather in the shade on the bottom of small canyons of the otherwise flat surface of the plateau.

Distribution

Heliamphora exappendiculata is restricted to the Chimanta-massif and Aprada-tepui. So far, most collections have been made from the central and northern parts of these features. It also has been recorded from the base and the top of Aprada-tepui. *Heliamphora heterodoxa* is only known from the top of Ptari-tepui and from the adjacent areas in the Sierra de Lema. All specimens collected from Chimanta-tepui as *H. heterodoxa* (like e.g. Steyermark & Wurdack 374 and 375) belong to the recently described new species *H. chimantensis*. From Auyan-tepui, Steyermark (1984) described a distinct form as "*Heliamphora heterodoxa* var. *exappendiculata* forma *glabella* (Steyermark)." The material was collected by Steyermark at the plateau of Auyan-tepui (J.A. Steyermark 93712, VEN). Closer examination of this specimen, however, revealed that in fact it

represents a highly etiolated *H. minor* plant. We also found material in Caracas labelled *H. heterodoxa exappendiculata* f. *glabella*, collected at the plateau of Aparaman-tepui. (Collected by Bruce Holst at 22.03.1987 (Holst 3485) for the Missouri Botanical Garden herbarium and determined by J.A. Steyermark.) It seems there was some confusion about the collected specimens of the Aparaman-group, because members of the same taxon were also determined as *H. heterodoxa* (Huber & Gorzula, 11.147, VEN), *H. heterodoxa* var. *exappendiculata* (Steyermark *et al.* 132045, VEN), or remained unidentified (Holst *et al.* 2923, VEN). Indeed all specimens currently known from the Aparaman-group belong to *H. folliculata*. These ambiguities can be resolved with current understandings of the new species that have been subsequently described, i.e. *H. exappendiculata* and *H. folliculata*. We hope, that in the future, the type-material for *Heliamphora exappendiculata* f. *glabella* (Steyermark 93712) can be found again for further examinations.

Morphology and Distinguishing Characteristics

Heliamphora exappendiculata can easily be distinguished from other *Heliamphora*-species because it is the only species where the lid is embedded in the surface of the pitcher. In contrast, *H. heterodoxa* has one of the most prominent lids in the whole genus. The pitchers of *H. exappendiculata* are infundibuliform, usually 12-15(25) cm long, whereas in *H. heterodoxa* the plant is in all parts tubular and 20-30(40) cm long. The flowers of *H. exappendiculata* are comparably large with elongated tepals, usually 1-2 flowered; in *H. heterodoxa* the flowers are comparably small with the shortest tepals in the genus, usually 2-4(7) flowers on each inflorescence. The ecological differences are also obvious—*H. exappendiculata* grows at or below vertical, wet cliffs, while *H. heterodoxa* grows exposed at the top of Ptari tepui or in open savannahs in the Sierra de Lema.

Relationships to Other Species

Heliamphora exappendiculata has no close similarities to *H. heterodoxa*, *Heliamphora pulchella*, which also grows at the Chimanta-massiv and on Aprada-tepui, shares with *H. exappendiculata* the short pitchers, but the other morphological characters of the pitchers, lid and flowers are clearly different (see Table 1). Furthermore, the habitats of *H. pulchella* (open bogs and swamps) are different from the habitats of *H. exappendiculata*. The other species from Chimanta-tepui that grows near *H. exappendiculata* is *H. chimantensis*. The pitchers of these two species are clearly different—those of *H. chimantensis* are tubular, elongated pitchers with a well developed lid. The flowers are also easily to distinguish; in *H. chimantensis* the tepals are shorter, lanceolate with broad base, in *H. exappendiculata* the tepals are larger, and oblong-lanceolate.

Morphologically, *H. exappendiculata* shows most affinities to the recently described *H. hispida* (Wistuba & Nerz), which grows about 500 kilometers away at the isolated Neblina-plateau. It has in common with *H. hispida* the short pitchers with a clearly infundibulate upper part, and also the flowers are similar with oblong-lanceolate tepals and 8-10 stamina. Furthermore, both species grow in colonies. But there are clearly differentiating characteristics between these species, e.g. the hairiness of the inner part of the pitcher, the absent lid in *H. exappendiculata*, and the different habitats, e.g. *H. hispida* never has been observed on vertical cliffs.

Etymology

The species epithet “*exappendiculata*” means “without appendage,” and notes the unique characteristic of this species.

Discussion

When Bassett Maguire and Julian A. Steyermark worked on the botany of the Guyana-shield of Venezuela, they had to treat a huge amount of field and herbarium work. When they started their expeditions, this extraordinarily rich flora was nearly unexplored, and even today many parts remain to be explored. It took from 1946, when *H. exappendiculata* was collected for the first time,

	<i>H. exappendiculata</i>	<i>H. heterodoxa</i>	<i>H. pulchella</i>	<i>H. hispida</i>
Pitcher				
Dimensions	12-25 cm long 4-10 cm wide	15-40 cm long 5-6 cm wide	8-20 cm long 3-8 cm broad	15-25 cm long 5-8 cm wide
Shape	Ventricose in the lower part, infundibulate to broad infundibulate in the upper part	Infundibulate to ventricose in the lower third, slightly infundibulate in the upper part, expanded near the mouth	Slightly ventricose in the lower part, narrowly expanded to tubular in the upper part	Slightly ventricose in the lower part, broad infundibulate in the upper part
Lid				
Dimensions	0.5-1 cm long 0.4-0.8 cm wide	1-3.5 cm long 1-1.5 cm wide	0.5-1 cm long 0.3-0.5 cm wide	1-1.5 cm long
Shape	Round to ovate, embedded in the apical end of the pitcher-surface, usually pointed in the apex	Strongly helmet-shaped, very constricted to stalked at the base	Flattened to helmet-shaped, only slightly constricted around the base	Cordate, curved
Inflorescence				
Dimensions	Peduncle 40 cm long, pedicels 3-5 cm long	Peduncle 30-70 cm, pedicels 5-6 cm long	Peduncle 20-40 cm long, pedicels 12 cm long	Peduncle 100 cm long, pedicels 12 cm long
Tepals	Oblong-lanceolate, narrowing near the base	Very broadly lanceolate	Lanceolate, broad base	Lanceolate, broad base
Anthers/ Stamens				
Dimensions	8 mm long	5.5-8mm long	4 mm long	3.5 mm long
Number	10	12	15	10
Table 1: Comparison between <i>H. exappendiculata</i> , <i>H. heterodoxa</i> , <i>H. pulchella</i> and <i>H. hispida</i>				

until 1978 for this outstanding species to be described. It was first described only as a variety of *H. heterodoxa*, perhaps because the authors—who were aware of its lack of a prominent lid—did not appreciate the other divergent characters. Its description merely notes that “*Var heterodoxi sinuili sed auplhoris sine appendicibus*” (“similar to var. *heterodoxa*, but pitchers without appendix”). Further, it was mentioned that “in the var *exappendiculata* the appendage has become completely or essentially lost, and the inner glandular area lowered to the apex of the leaf”. It seems that the authors only concentrated on the most obvious characteristics—the lacking lid—but were not aware of the other distinct characters of this species, which make it very different from *H. heterodoxa*. Steyermark (1951) wrote of *H. heterodoxa* as being a variable species, but the specimen used to justify this characterization (i.e. Steyermark 59766, with somewhat more infundibulate pitchers) might have been collected in more shaded habitats. In actuality, *H. heterodoxa* is only a moderately variable species. The specimens at the top of Ptari-tepui are narrower near the mouth and more

colourful, compared to the usually greenish specimens that occur in the Gran Sabana or in shaded habitats. In these areas they are somewhat more infundibuliform. Steyermark also felt that *H. heterodoxa* was a variable species because of two other collections, i.e. Steyermark & Wurdack 374, and Steyermark & Wurdack 375. However, these specimens belong to the recently described species *H. chimantensis*. When these incorrectly placed specimens are removed from inclusion with *H. heterodoxa*, the species is seen as being not very variable at all.

We can conclude that *H. exappendiculata* is one of the most distinct and interesting *Heliamphora* species, and one that can be identified clearly on the first sight.

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